

THE ABDOMINAL STRUCTURES OF THE ORTHOPTEROID FAMILY GRYLLOBLATTIDÆ AND THE RELATIONSHIPS OF THE GROUP

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Mr. Eric Hearle and Prof. Owen Bryant have generously supplied me with a fine series of Grylloblattid material, including practically all of the developmental stages of *Grylloblatta campodeiformis* Walk., and, through the kindness of Mr. H. S. Barber, I have been able to obtain from a Californian collector a full-grown female nymph of *Grylloblatta barberi* Caudell. During a visit to the National Museum I had an opportunity of making sketches of an immature male of *Grylloblatta barberi* and a male of *Galloisiana* (*Galloisia*) *nipponensis* Cdll., through the kindness of Mr. A. N. Caudell, to whom I am likewise indebted for many favors in the past. To all of these gentlemen I would express my deep appreciation of their kindness, which has made this investigation possible.

The Grylloblattids are of such great interest and importance for the study of the Orthopteroid insects in general, that all of the features of Grylloblattid anatomy should be made available to entomologists who have an interest in the evolution and natural grouping of the insects with which they have to deal. There are no figures of the details of the entire abdomen of a Grylloblattid, however, and the terminal abdominal structures of the two sexes of *Grylloblatta barberi* have never been figured, so that the present paper is offered with a view to supplying some of this needed data; and the evidence of relationships furnished by the other parts of the body is also briefly reviewed in this paper.

According to Caudell, 1924, the differences between the Grylloblattid genera *Galloisiana* and *Grylloblatta* include the following features: (1) The presence of the posterior process (labeled *poc* in Fig. 2) in the male of *Galloisiana*, a process which is lacking in all of the recorded species of *Grylloblatta*. (2) The occurrence of stouter spines in *Galloisiana*, and slenderer ones in *Grylloblatta*. (3) The absence of a chitinous process on the dextral coxite of males of *Galloisiana*, and its presence in adult males of *Grylloblatta*. (4) The occurrence of nine segments in

the cerci of *Galloisiana*, as against eight in the cerci of *Grylloblatta*. (5) The occurrence of forty segments in the antennæ of *Galloisiana*, as against about thirty (as a maximum) in *Grylloblatta*. (6) The presence of large flange-like tarsal pads in *Galloisiana*. Mr. Caudell is apparently quite justified in erecting a new genus (*Galloisia*, which was later changed to *Galloisiana* because *Galloisia* was preoccupied) for the Japanese species because of these differences, but I think that he is wrong in maintaining that there are no tarsal pads at all in *Grylloblatta*, because in my material of this genus preserved in alcohol there are distinct tarsal pads like those labeled *tp* in Fig. 3.

Caudell, 1924, considers that the immature specimens of *Grylloblatta* recently captured in California by Mr. H. S. Barber belong to a distinct species which Caudell has called *Grylloblatta barberi*. Mr. Caudell is apparently fully justified in considering the Californian forms as the representatives of a new species (despite the fact that only their immature stages are known) since, among other differences, the sinistral coxite (*cxi* of Fig. 8) of an immature male of *Grylloblatta barberi* is much slenderer than the corresponding left coxite (*cxi* of Fig. 5) of an immature male of *Grylloblatta campodeiformis*, and the coxites differ markedly in shape in the two insects. Since the coxites do not change greatly as the male Grylloblattids become mature, these differences will doubtless hold good in the adult stages as well.

In comparing the terminal abdominal structures of an immature male of *Grylloblatta* (Fig. 5) with an immature female of the same species (Fig. 9) it is apparent that the coxite *cxi* of the ninth abdominal segment or uromere of the male (Fig. 5) corresponds to the elongated coxite, coxite *dv* of the ninth uromere of the immature female (Fig. 9), and the styli *st* of the male (Fig. 5) are likewise homologous with the styli *st* of the female (Fig. 9). There are no appendages of the eighth uromere or abdominal segment of the male corresponding to the appendages of the eighth uromere of the female.

Doctor Walker maintains that, with the exception of female Odonata, male Grylloblattids are the only Pterygotan insects which retain distinct, styli-bearing coxites in their adult stages, and I formerly held the same opinion. Recently, however, in studying the genitalia of insects related to the Hemiptera and

the members of the Holometabolous orders, I have found distinct styli-bearing coxites in the females of certain Lampyroid Coleoptera, in certain Hemiptera, etc., and such structures are apparently of wider occurrence than either of us realized and statements concerning their occurrence need revision. Since these styli-bearing structures occur in adults of the above-mentioned insects, it is not wholly improbable that the ancestors of the Grylloblattids exhibited distinct styli-bearing coxites in the adult stages of both sexes, while only the males of *Grylloblatta* exhibit them in the adult condition at the present time.

When the female nymphs of *Grylloblatta* become adult the following changes take place in the ovipositor and the region at its base: the stylus *st* (Fig. 9) of the nymph is lost, and the elongated coxite *dv* (Fig. 9) of the nymph becomes the dorsal valve *dv* of the adult (Fig. 10). The inner valve *iv* (Fig. 9) of the nymph becomes the inner valve *iv* (Fig. 10) of the adult, and the ventral valve *vv* (Fig. 9) of the nymph becomes the ventral valve *vv* (Fig. 10) of the adult. The small coxite *bv* (Fig. 9) of the eighth uromere (abdominal segment) of the nymph takes part in the formation of the basivalvula *bv* (Fig. 10) of the adult, and the region of the ninth sternite bearing the label *vf* in Fig. 9 of the nymph, becomes the valvifer *vf* of the adult insect shown in Fig. 10.

From the foregoing it is evident that it is a comparatively easy matter to compare the parts of an adult female with those of an immature female, and it is also comparatively easy to homologize the parts of both of these with the parts of the male insect. It is somewhat more difficult, however, to interpret the parts of the ovipositor in terms of the primitive biramous Crustaceoid limb (i. e. a limb composed of a basal portion or propodite bearing an outer branch or exopodite, and an inner branch or endopodite) because the different investigators are not agreed as to whether the inner valves of the ovipositor belong to the ninth or to the tenth uromere (abdominal segment). Walker, however (whom I have followed in these matters), considers that the inner valves belong to the ninth uromere, and if this be correct the parts of the ovipositor of the female nymph may be interpreted in terms of a biramous appendage in the following fashion; the elongated coxite *dv* of Fig. 9 represents the propodite of a biramous limb of the

ninth abdominal segment, in which the exopodite forms the stylus *st* and the endopodite forms the intermediate valve *iv*. The short coxite *bv* of Fig. 9 represents the protopodite of the limb of the eighth abdominal segment, which has lost its exopodite or stylus, but has retained its endopodite, represented by the ventral valve *vv* of Fig. 9. In the adult female (Fig. 10) the dorsal valve *dv* would then represent the elongated coxite or protopodite of a biramous limb of the ninth uromere, which loses its stylus or exopodite when the insect becomes mature, but this limb of the ninth uromere retains its endopodite to form the inner valve *vv* of the adult shown in Fig. 10. The sclerite *vf* of Fig. 10 is merely a portion of the sternum of the ninth uromere bearing the dorsal (*dv*) and inner valve (*iv*) of the ovipositor. The parts of the eighth segment have the following interpretation. The coxite or protopodite of the limb of the eighth uromere forms the sclerite *bv* of Fig. 10, and the endopodite of the limb of the eighth uromere is retained to form the ventral valve *vv* of the ovipositor of the insect shown in Fig. 10. The limb of the eighth uromere has no stylus (exopodite) so that this structure is not represented in the eighth uromere of the nymph or adult insect. In the male insect (Fig. 8) the coxite *cxi* represents the protopodite of the limb of the ninth uromere, and the stylus *st* represents its exopodite. The endopodite of the limb of the ninth uromere may be represented by the parameres, but this point has not been definitely determined.

The parapodial plates or paraprocts *pa* of Figs. 8, 9, 10, etc., apparently represent the coxites or modified protopodites of the limb of the eleventh (or tenth) abdominal segment, whose exopodite is lost and whose endopodite forms the cercus *ce*. At any rate, the cercus develops exactly like the thoracic limbs in the embryo according to Wheeler, Heymons and other embryologists, and since the limbs of the thorax are acknowledgedly endopodites, this would indicate that the cerci also represent endopodites rather than exopodites (see Crampton, 1921), and the condition exhibited by certain Crustacea also lends weight to this view, which is discussed more at length in the paper cited above.

Since *Grylloblatta* is such a primitive Orthopteran, I had hoped that it would throw some light on the question as to

whether the epiproct *ep* of Figs. 8 and 9 represents the tenth tergite, or the tenth tergite and eleventh tergite united to form an apparently single sclerite; but there is no indication of a transverse division of the epiproct in *Grylloblatta* despite the fact that certain other Orthoptera show some indications of such a division. Furthermore, none of the stages of *Grylloblatta* in my series shows any indication of the presence of a twelfth segment or telson, and I must confess that I am extremely skeptical as to the correctness of the claims of those who profess to be able to find traces of a twelfth "segment" or telson in the postembryonic stages of any Pterygotan insect (although twelve segments occur in the abdominal region of the Protura). The membranous rectal lining labeled *er* in Figs. 9 and 10, has become everted in some of the specimens thrown into alcohol while still alive, but this rectal lining can hardly be interpreted as the remains of a twelfth segment. The rectal lining is frequently everted in Psocids, Isoptera, and related forms, if the specimens were thrown into alcohol, and it would be of some interest to determine whether this eversion of the rectum is the result of the action of the preserving fluid, or whether (as is more probably the case) it is caused by the irritation set up by the alcohol, etc. There have been no experiments to determine whether the eversion of the rectal lining is in any way associated with repelling enemies, and it would be interesting to know if there are any repugnatorial glands in this region. The fact that this eversion of the rectal lining occurs in Isoptera, Grylloblattids, Gryllotalpids, Psocids, etc., has some significance in indicating a relationship between the insects in question, as will be discussed later.

Mr. Caudell apparently considers that none of the described species of *Grylloblatta* is adult; but Miss Ford has described the mating, egg-laying, etc., of *Grylloblatta campodeiformis*, and no one who has made a study of the genitalia of the males and the abdomen of gravid females of *Grylloblatta campodeiformis* can doubt the maturity of these forms.

The abdomen of a gravid female of *Grylloblatta campodeiformis* is shown in Fig. 10. The abdomen of the specimen there figured was abnormally distended due to the action of the fluid in which it was preserved; but the specimen in question is extremely well chitinized and pigmented, and the parts are

exceptionally favorable for study, and I have, therefore, made it the basis of the drawing shown in Fig. 10. The tergites and sternites are quite widely separated in the specimen in question, and the membranous regions of the abdomen are apparently capable of considerable distention. The third to the sixth tergites (inclusive) are the broadest, and the seventh sternite is the longest.

As is shown in Fig 4, the first sternite 1^s is separated from the posterior region *ss* of the metasternum by a membranous area, instead of being closely associated with the metasternum, as is the case in the first sternite of other Orthoptera. Beneath the first sternite is an eversible sac bearing the label *pr* in Figs. 1, 4 and 10, and this structure probably functions as a repugnatorial "gland." In the nymph of *Grylloblatta barberi* shown in Fig. 1, the everted sac is rather slender. In the adults of *Grylloblatta campodeiformis* shown in Figs. 4 and 10, the structure in question is somewhat larger, and the "gland" may be better developed in the adults than in the nymphal stages.

In some specimens of *Grylloblatta campodeiformis* there are slight indications of a deposition of chitin and pigment about the proximal spiracles; but for the most part the spiracles lie in the membrane near the margins of the tergites as shown in Fig. 10. The abdominal spiracles of the Grylloblattids are very small, and are rather difficult to detect.

The egg shown in Fig. 6 is about one and five-sevenths mm. long and five-sevenths mm. broad. It is black in color, is somewhat more rounded at the posterior(?) end, and is slightly more pointed at the anterior (?) end. The supposedly ventral side is directed toward the top of the page in Fig. 6, and is somewhat more convex than the opposite side of the egg. In the region *m*, which may represent the micropylar end, the tiny processes (which occur at the opposite end of the egg also) on the surface of the egg give a roughened appearance to this area. The eggs are laid singly, and are probably deposited in moss or similar substances during the nocturnal wanderings of the female.

The fact that Grylloblattids raise the abdomen high above their heads when irritated, indicates that they are "psychically" allied to the Dermaptera, but their egg-laying behavior is "out-and-out" Orthopteran. Their nocturnal habits, and their ten-

dency to hide under stones, logs, etc., are shared alike by the earwigs and certain Orthoptera.

In color the Grylloblattids are very suggestive of Phasmids such as *Timena*, or certain of the paler earwigs. They also approach certain termites in the color of the body in general, and I think that these features, as well as the structures of the body, etc., are of some value in indicating their relationships and evolution, as will be presently discussed.

Before taking up the discussion of the relationships indicated by the various anatomical structures of the Grylloblattids, I would call attention to the method of grouping the Orthopteroid insects (i. e., the Paurometabola or Orthopteradelphia) into superorders representing the natural relationships of the insects in question, as indicated by comparative anatomy, the palaeontological record, and other features. There are three principal superorders of Orthopteroid insects, as follows: (1) The *Panisoptera*, including the fossil Protoblattids, Blattids and Mantids, Isoptera, etc. (2) The *Panplecoptera*, including the fossil *Hadentomoidea*, Embiids, Plecoptera, etc. (3) The *Panorthoptera*, including the fossil Protorthoptera, Grylloblattids and Saltatoria, Phasmids, Dermaptera, etc. All of these insects were apparently descended from common ancestors in the common Protorthopteran-Protoblattid stem (see Textfigure A which gradually split into the Protoblattids (which retained most of the ancestral features of the group) and the Protorthoptera. Although all three superorders were derived from ancestors in the common Protorthopteran-Protoblattid stem, the ancestors of the Panorthoptera and Panplecoptera were probably somewhat more Protorthopteroid, while the ancestors of the Panisoptera were probably slightly more Protoblattoid, although all three groups naturally merge, as we trace them to their ultimate origin in the common Protorthopteran-Protoblattid stem.

The common ancestors of all of these forms in the common Protorthopteran-Protoblattid stem may have exhibited the following characteristics: They were possibly nocturnal or tended to hide under stones, logs, etc. The color was probably yellowish brown. Head prognathous and Plecopteroid or Dermapteroid (i. e., like that of an earwig, with eyes on side of head, antennæ borne below the eyes, near the base of the man-

dibles, etc.) and provided with three ocelli. Temporal sutures probably present, demarking the temporal regions from the parietals. The proximal segments of the antennæ were doubtless much shorter than the distal ones, which tended to become more elongated and cylindrical. The cervical sclerites were well developed in the lateral region of the neck, and in the prothorax the trochantin intervened between pleural region and the coxa. The pleural suture was continued downward into the trochantinal region, and the trochantin was divided into several areas by sutures, clefts, etc. The pronotum was demarked into a small anterior region and a larger posterior one by a transverse suture. The spinisternal region of the prothorax was closely associated with the spiracles. The meso- and metathorax were subequal, although the metathorax tended to surpass the mesothorax in size, and the hind wings tended to become larger than the fore wings, and doubtless bore an anal fan. A distinct laterosternite was present in both meso- and metathorax, and the coxæ were Blattoid. The tarsi were pentamerous, and tarsal pads or "soles" were probably present on all segments of the tarsi. The ovipositor of the female was probably rather short, but was not concealed by a hypogynium, or subgenital plate, and the valves of the ovipositor were subequal in length. In the immature females the dorsal valves bore styli, and it is barely possible that these were retained even in the adult stages. In the males separate and distinct styli-bearing coxites were borne in the posterior region of the hypandrium or ninth sternite, and the phallus or copulatory portion of the genitalia was probably composed of lobe-like structures provided with accessory chitinous outgrowths, etc. The paraprocts were well developed, and the epiproct may have been divided by a transverse suture or similar division line. The cerci were composed of a number of segments, and the distal ones tended to become more elongated and cylindrical. From ancestors in the common Protorthopteran-Protoblattid stem exhibiting characters like those described above were descended the Grylloblattids and their Orthopteroid relatives. The Grylloblattids have retained many of these ancestral features, and they combine in themselves certain characters found in other Orthopteroids, making the study of their anatomy of the greatest importance from the standpoint of phylogeny. The most important of these features,

and the relationships indicated by them, may be briefly indicated as follows:

(1) ANTENNÆ. As described by Crampton, 1917_a, the antennæ of *Grylloblatta* are strikingly similar to those of *Embia*, and resemble the antennæ of such primitive Phasmids as *Timema* very markedly. The Acridoidea (i. e., Acrididæ, Tettigidæ, Tridactylidæ, etc.), have antennæ resembling those of *Grylloblatta* more closely than is the case with the antennæ of the Grylloidea and Tettigonioida. This probably indicates that the ancestors of the Acridoidea, Grylloblattids, Embiids, certain Phasmids, etc., had antennæ like those of *Grylloblatta*, although some of the ancestral Orthopteroid types undoubtedly had antennæ more like those of roaches, Mantids, crickets, Tettigoniids, etc.

(2) HEAD CAPSULE. The head capsule of *Grylloblatta* is markedly Dermapteroid, as was pointed out by Crampton, 1926_a. The head capsule of the Embiids, Phasmids, and Plecoptera are essentially of this type, and all of these have retained this primitive type of head capsule from their common ancestry. The head capsule of these forms is much more like that of *Lepisma* (and is therefore more primitive) than is the head capsule of the Blattids and Mantids.

(3) LABIUM. The underlip of *Grylloblatta* is Orthopteroid according to Crampton, 1926_a, and resembles the underlip of the Gryllids and Tettigoniids very closely. The evidence from this source would indicate that *Grylloblatta* is an Orthopteron, or a member of the superorder Panorthoptera, and probably inherited this type of labium from the common Protorthoptera-like forebears of the Panorthoptera.

(4) NECK AND PROTHORAX. The neck plates of *Grylloblatta* are Orthopteroid (see Crampton, 1926_b), and they are also very suggestive of the neck plates of the Isoptera in many respects. The pronotum, with its transverse suture, is very like that of certain Dermaptera, Embiids, etc., and the propleuron is strikingly similar to that of the Dermaptera and Embiids, but also shows Isopteroid affinities. These facts are in accord with the evidence from other sources indicating that the Isoptera are very like the Protoblattoid ancestors in the common

Protorthopteran-Protoblattid stem giving rise to the lines of descent of the Protorthoptera, Grylloblattids, Dermaptera, Embiids, etc., and the more immediate ancestors of the latter groups were probably Protorthopteroid in character.

(5) MESOTHORAX AND METATHORAX. The thoracic sclerites of *Grylloblatta* were discussed by Crampton, 1915, but the analysis of the relationships indicated by the thoracic structures is much better presented in later papers. *Grylloblatta* together with the Isoptera and Zorapterous Psocids are the only insects of which I have any knowledge, in which a separate and distinct laterosternite occurs in both meso- and metathorax. This would be in line with other evidence indicating that the Isoptera approach the Protorthopteroid ancestors of the Grylloblattids, and these Protorthopteroid ancestors of the Grylloblattids were identical with, or were very closely related to the Isoptera-like, Protorthopteroid ancestors of the Psocids. Although the fact is not noted in the earlier papers, it is quite apparent that the pleural region labeled *lp* in Fig. 10 is an Isopteroid feature representing the so-called lateropleurite of the meso- and metathorax of certain Isoptera; and the character of the trochantin *tn* of Fig. 10 is very Isopteroid (although it is also Blattoid and Mantoid as well). The evidence of the thoracic sclerites would indicate that the Isoptera approach the Protorthopteroid ancestors of the Grylloblattids, Dermaptera, Embiids, etc., more closely than the Blattids and Mantids do, and many features in the thorax indicate that the Dermaptera and Embiids were descended from a Protorthopteroid ancestry identical with that of the Grylloblattids, although the Embiids tend to accompany the Plecoptera more closely in their evolutionary tendencies, as the ancestors of both of these groups began to develop away from the ancestral Grylloblattids.

(6) LEGS. As was pointed out by Crampton, 1915, the coxæ of *Grylloblatta* are of the type occurring in Blattids, Mantids, and wingless Isoptera. This Blattoid type of coxa is probably the ancestral one for the superorders Panorthoptera and Panplecoptera, and the Zorapterous Psocids were probably descended from forms having coxæ somewhat like those of *Grylloblatta*. The pentamerous tarsi of the Mantids are very like those of the ancestors of the Grylloblattids, and some Man-

tids have flange-like tarsal pads very suggestive of those occurring in *Galloisiana* and in certain Gryllacrids. I now consider that the trimerous tarsi of Embiids, Plecoptera, etc., are secondary (the tarsal pads of Embiids, for example, indicate that the tarsi were originally composed of more than three segments) and the pentamerous type represents the ancestral one for these insects also. *Grylloblatta* apparently inherited its tarsal "pentamerism" from its Protorthopteroid ancestors in the common Protorthopteran-Protoblattid stem, and the Phasmids did the same; but the other members of the superorders Panorthoptera and Panplecoptera tend to lose the ancestral "pentamerism." In lacking a developed arolium, *Grylloblatta* has retained a condition suggestive of affinities with the Isoptera and Dermaptera; but certain Gryllacrid Orthoptera have also not developed an arolium, and it is quite possible that the ancestral Orthopteroids may have been of two types, one developing an arolium, and the other lacking it. It is uncertain whether or no the common ancestors in the common Protorthopteran-Protoblattid stem had an arolium, although it is not impossible that some had an arolium and others did not, at a very early stage of Orthopteroid development.

(7) ABDOMEN. The abdominal sclerites of *Grylloblatta* are Orthopteroid and indicate that *Grylloblatta* is a true member of the superorder Panorthoptera. There is something very suggestive of Isopteran affinities in the character of the sclerites in general in the abdomen of *Grylloblatta*, but it is difficult to say what these Isopteran characters are in regions other than the terminal segments — which show more than a hint of Isopteran affinities. The general outlines of the tergites and sternites of *Grylloblatta*, and the character of the parapodial plates, supra-anal plate, etc., are quite Isopteroid; but the Mantids also resemble the Grylloblattids in these features, and the ovipositor of the Mantids is much more like that of *Grylloblatta* than is the case with the ovipositor of such primitive Isoptera as *Mastotermes*, for example. Thus, while the Isoptera have retained certain features which doubtless occurred in the ancestors of the Grylloblattids, the Mantids have retained more of the ancestral features in the abdominal region.

(8) OVIPOSITOR. The ovipositor of *Grylloblatta* is entirely Orthopteroid, as was pointed out by Crampton, 1917_b. Walker,

1919, however, gives a much better description of the ovipositor of *Grylloblatta*, and compares its parts with those of other Orthopteroid insects, although he apparently uses the term "Orthopteroid" to include Odonata and other forms not related to the Orthoptera in the sense indicated by the use of the term Orthopteroid in this paper. Not only is the ovipositor of adult Grylloblattids clearly Orthopteroid, but the styli-bearing dorsal valves of nymphal Grylloblattids are paralleled by the the styli-bearing dorsal valves of the ovipositors of certain Orthoptera as well. The ovipositors of nymphal Grylloblattids, however, remind one somewhat of the ovipositors of nymphal Blattids, Mantids, and soldiers of the termite *Mastotermes*, and the ovipositor of adult Mantids is very like the ovipositor of an adult Grylloblattid. These members of the superorder Panisoptera have apparently retained the fundamental type of ovipositor occurring in the common ancestors of the Panisoptera, Panorthoptera and Panplecoptera in the common Protorthopteran-Protoblattid stem. The members of the superorder Panplecoptera, however, have lost the ovipositor, and they are consequently less like the common ancestral type in this respect.

(9) MALE GENITALIA. Walker, 1919 and 1922, gives a fine description of the genitalia of *Grylloblatta*, which he likens to the genitalia of the Blattids and Mantids. The genitalia of *Grylloblatta* are of a somewhat more primitive type than those of the Blattids and Mantids, and the Grylloblattids have apparently retained the genitalia in a condition approximating the ancestral type more closely than any other members of the Orthopteroid superorders, although the Grylloblattids have naturally developed certain specializations of their own, as would be expected. Although the genitalia of the Grylloblattids resemble those of the Blattids and Mantids quite closely, they are evidently very like the type at the basis of the Orthopteroid forms and resemble those of the Phasmids very closely. The genitalia of the Embiids and Plecoptera have apparently departed further from the ancestral type, and have developed along their own lines of specialization. The Phasmids are remarkably similar to the Grylloblattid type in their genetalic features, but the Dermaptera do not resemble the Grylloblattids in these features as much as one would expect from the marked resemblance between the Dermaptera and Grylloblattids in other

respects. The Isoptera have also developed along their own lines of specialization (the male genitalia are not developed in those which I have examined); and all of these facts probably indicate that the genitalia are not equally modified in all of the orders of insects, and while they may be of value for indicating affinities in some groups, they are of less value in others.

(10) CERCI, PARAPROCTS, etc. As was pointed out by Crampton, 1917_b, the cerci of *Grylloblatta* are Plecopteroid in many respects, and they also resemble the type of cerci occurring in the immature stages of such Dermaptera as *Discrytina*. The cerci of the primitive termite *Archotermopsis* are likewise extremely like those of the Grylloblattids, and the cerci of certain Blattids and Mantids are somewhat suggestive of the type occurring in *Grylloblatta*. This probably indicates that the cerci of the common ancestors of the Panorthoptera and Panplecoptera were Plecopteroid in certain respects, and the termites approach these common ancestors in this respect somewhat more closely than the Blattids and Mantids do. The epiproct and paraprocts bearing the labels *ep* and *pa* in Figs. 8, 9, 10, etc., of *Grylloblatta* are decidedly Orthopteran, and add their evidence to that of other features indicating that the Grylloblattids are Orthoptera, or should be grouped in the superorder Panorthoptera. The epiproct and paraprocts of the Grylloblattids are also very like those of the Isoptera, and resemble these structures in the Mantids as well. This is in line with the evidence from other sources indicating that the Grylloblattids are extremely closely allied to the Orthoptera, and that the Isoptera approach the ancestors of the Grylloblattids in many respects, as is also true of the Mantids, although the Mantids are in general somewhat less like these ancestors than the Isoptera are.

(11) COLOR. The color of the Grylloblattids is a yellowish brown (or brownish yellow) and is very suggestive of that of certain termites. The color of the Grylloblattids is also very like that of certain Phasmids related to *Timema*, and one species of *Timema* is extremely like *Grylloblatta* in its general appearance. The Dermaptera are usually darker in color than the Grylloblattids are, but some of the earwigs also resemble the Grylloblattids in this respect. A few roaches and Mantids and some Plecoptera are brownish yellow, and some Embiids

are also yellowish brown in color, but on the whole the termites are nearest the Grylloblattids in this feature. Certain Tettigoniids and some of the Gryllids are colored like *Grylloblatta*, and these facts seem to indicate that the common ancestors in the common Protorthopteran-Protoblattid stem may have been yellowish brown or brownish yellow in color.

(12) BEHAVIOR, etc. Certain Tettigoniids such as *Ceuthophilus* and many crickets hide under stones, logs, etc., and share with *Grylloblatta* its habits of concealment; and most Tettigoniids are nocturnal, as are the Cæcanthids and other Orthopteran relatives of the nocturnal Grylloblattids. The Dermaptera are nocturnal or hide under stones, etc., and Embiids hide in their tunnels thus exhibiting a tendency in this direction, and even the Plecoptera exhibit a tendency to hide in crevices, etc. The Isoptera as a group live in protected situations, and of course the roaches are nocturnal and hide under stones, in crevices, etc. These facts may be interpreted as indicating that the common ancestors of all these insects (i. e. the common Protorthopteran-Protoblattid stem) were probably nocturnal or tended to hide under stones, logs, etc. The "embarrassment" reaction of nibbling the foot, cleaning the antennæ, polishing the head and similar elaborate actions of "unconcern" upon coming "face to face" with one of its own kind is exhibited by the Grylloblattids and related Tettigoniids such as *Decticus*, etc., and evidently indicates a similar "physico-chemical" makeup in the nervous system of these insects. The reactions of *Grylloblatta* to a light brought near them in captivity are suggestive of those of roaches under similar conditions and much of its behavior is suggestive of "psychic affinities" with the roaches. The habit of holding the abdomen high over the head when irritated is shared alike by Grylloblattids and Dermaptera, and is such a peculiar reaction that it undoubtedly indicates a rather close relationship between the Dermaptera and Grylloblattids. The egg-laying habits of *Grylloblatta* are clearly Orthopteran, and the eggs are extremely like those of the Orthoptera, so that taking it all in all the evidence thus far available would indicate that the closest affinities of the Grylloblattids are with the Orthoptera, while they are somewhat less closely allied to the Dermaptera and Phas-

mids and still less so to the Embiids and Plecoptera. The Isoptera are their closest allies among the Panisoptera, and the Blattids and Mantids are slightly further removed, the Mantids being somewhat nearer than the Blattids are to the Protoblattid-like forms giving rise to the Protorthopteroid ancestors of the Grylloblattids and other members of the superorder Panorthoptera.

The principal points brought out in the foregoing discussion may be briefly summarized, as follows: All of the Orthopteroid insects (*sensu lato*) were ultimately derived from ancestors in the common Protorthopteran-Protoblattid stem, and these common ancestors were probably dark-loving forms hiding under stones, logs, etc. They were yellow brown (or brownish yellow), slender-bodied forms (Plecopteroid or Dermapteroid) having Dermapteroid heads, Isopteroid thoraces and coxæ, pentamerous tarsi, and hind wings with an anal fan. The abdomen was probably Grylloblattoid, or somewhat Mantoid, with Plecopteroid cerci.

From ancestors exhibiting the characters mentioned above were derived the Orthopteroid superorders; and the ancestors of the Psocoids, Holometabola, etc., were also very like these forms. As shown in Textfigure A, the Synarmogoidea connect these ancestral forms with the Palæodictyoptera (which in turn were derived from *Lepisma*-like ancestors) and these ancestral forms give rise to three main evolutionary groups. The first to branch off were the Protoblattids and their allies the Blattids and Mantids (i. e. the order Dictyoptera) and the Isoptera. The immediate ancestors of this group were somewhat more Protoblattoid than Protorthopteroid; but the immediate ancestors of the next two groups were somewhat more Protorthopteroid than Protoblattoid, and from such forms there developed in one direction the Embiids, Plecoptera and Hadenomoidea, while in the other direction were evolved the lines of descent of the Orthoptera, Phasmids, Dermaptera, and Protorthoptera.

In Textfigure B, I have endeavored to show the relationships of the Grylloblattids to the principal families of the order Orthoptera, although all of the Orthopteran families are not given in the tree there represented. The trees represented in Textfigures A and B should indicate that the branches are given off in three planes, but not knowing how to show this in the

figure, I shall merely call attention to the fact that a figure drawn in one plane does not correctly indicate the interrelationships of the lines of descent so depicted. Furthermore the Grylloidea (i. e. Gryllids and Gryllotalpids) are not the lowest representatives of the Orthoptera, as the figure might be taken to indicate, but the lines of descent of these forms were represented in this way to avoid crossing or overlapping in the figure.

As is indicated in Textfigure B, the Grylloblattidæ occupy a position at the base of the lines of descent of the Grylloidea and Tettigonioidea (or Locustoidea as they were formerly called). The Grylloblattids have departed but little from the Protorthopteroid ancestors of the Orthoptera in general, and their nearest relatives are the Tettigonioidea, the lowest representatives of which are the Gryllacridæ. The Grylloidea are almost as closely related to the Grylloblattids as the Tettigonioidea are, but on the whole the Tettigonioidea are somewhat nearer to the Grylloblattids than the Grylloidea are.

The fossil Elcanidæ may be related to the Tridactylidæ, although they exhibit certain features suggestive of a closer relationship to the Tettigonioidea. The Tridactylidæ have retained some features suggestive of the Gryllidæ from their ancient common ancestry, but the closest affinities of the Tridactylidæ appear to be with the Acridoidea and they approach the Acridoid family Tettigidæ in certain respects. The antennæ, tarsi, wings, ovipositor, etc., of the Tridactylidæ are certainly not Grylloid in appearance, but are very suggestive of the Acridoids in these respects, and the Tridactylidæ apparently occupy a position near the base of the lines of descent of the Acridoid families, as is indicated in the figure. The Tettigidæ are rather primitive Acridoidea in some respects, and their line of descent approaches that of the Tridactylids, but the closest affinities of the Tettigids are with the Acridids (and Pneumonids). The fossil family Locustopsidæ is rather like the ancestors of the Acrididæ, but we do not know enough about the ancestors of the Acridoidea (or Locustoidea as they are sometimes called) to do more than indicate their lines of descent in a general way, as shown in the diagram. The Grylloblattids have retained some ancestral features suggestive of those occurring in the primitive Acidoidea, but the closest affinities of the Grylloblattids are with the Tettigonioids and Grylloids, as was mentioned

above. In some respects the Grylloblattidæ are like living Protorthoptera, but they have also retained some features suggestive of an ancestry in forms more primitive than the Protorthoptera themselves, so that their line of descent is represented in Textfigure B, as though it sprang from the common Protorthopteran-Protoblattid stem from which the Protorthoptera also arose. The Grylloblattids, however, are probably true Orthoptera, although I formerly considered that they might represent a distinct order, the Archorthoptera or Notoptera. The principal superfamilies of the order Orthoptera, with their principal families would be grouped, as follows: (1) the Grylloblattoidea (with the single family Grylloblattidæ); (2) the Tettigonioidea (including the Gryllacrididæ, Stenopelmatidæ, Tettigoniidæ and Phasmodidæ, the latter are not to be confused with the Phasmidæ); (3) the Grylloidea (including the Gryllidæ and Gryllotalpidæ); (4) the Acridoidea (including the Tettigidæ, Pnueumonidæ, Acrididæ and Proscopidæ, to which the Locustosidæ might be added, and the Tridactylidæ and possibly the Elcanidæ might likewise be grouped in this superfamily, although the Elcanidæ probably belong with the Tettigonioidea). The Grylloblattoidea, Tettigonioidea, and Grylloidea belong in the suborder Euorthoptera, while the Acridoidea constitute the suborder Metorthoptera quite sharply differentiated from the Euorthoptera.

The anatomical features of *Grylloblatta* were more or less correctly portrayed in my earlier papers dealing with the morphology of this insect, and the structures figured were correctly homologized for the most part; but in these earlier papers the interrelationships of the Orthopteroid orders were not always indicated correctly, as a wider knowledge of the forms in question has shown. I would therefore emphasize the fact that the views expressed in the present paper are more nearly in accord with the facts revealed by a further study of a wider range of structures in the more primitive representatives of the orders in question, which were not available to me before. In subsequent papers I am hoping to take up a more detailed study of the parts not already described in the Grylloblattids, giving particular attention to the evidence of relationships furnished by the various anatomical features of these extremely interesting and important insects.

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ABBREVIATIONS

bs.—Basisternum	m.—Supposed micropylar region of egg
bv.—Basivalvula (a modified coxite)	pa.—Paraprocts, or parapodial plates
ce.—Cercus	pc.—Pericercal pores
cp.—Curvipleurite	poc.—Postcornu, or posterior process
cx.—Coxa	pr.—Primirepugnatorium or repugnatorium of first uromere
cxi.—Coxite	s.—Sternites
dv.—Dorsovalvula, or dorsal valve of ovipositor	sp.—Spiracles
em.—Epimeron	ss.—Spinasternum
ep.—Epiproct, or supra-anal plate	st.—Stylus
es.—Episternum	t.—Tergites
er.—Endorectum, or endorectal lining	tn.—Trochantin
fs.—Furcasternum	tp.—Tarsal pads
iv.—Intervalvula, or intermediate valve of ovipositor	vf.—Valvifer
lo.—Phallic lobes	vv.—Ventrovalvula, or ventral valve of ovipositor
lp.—Lateropleurite	
ls.—Laterosternite	

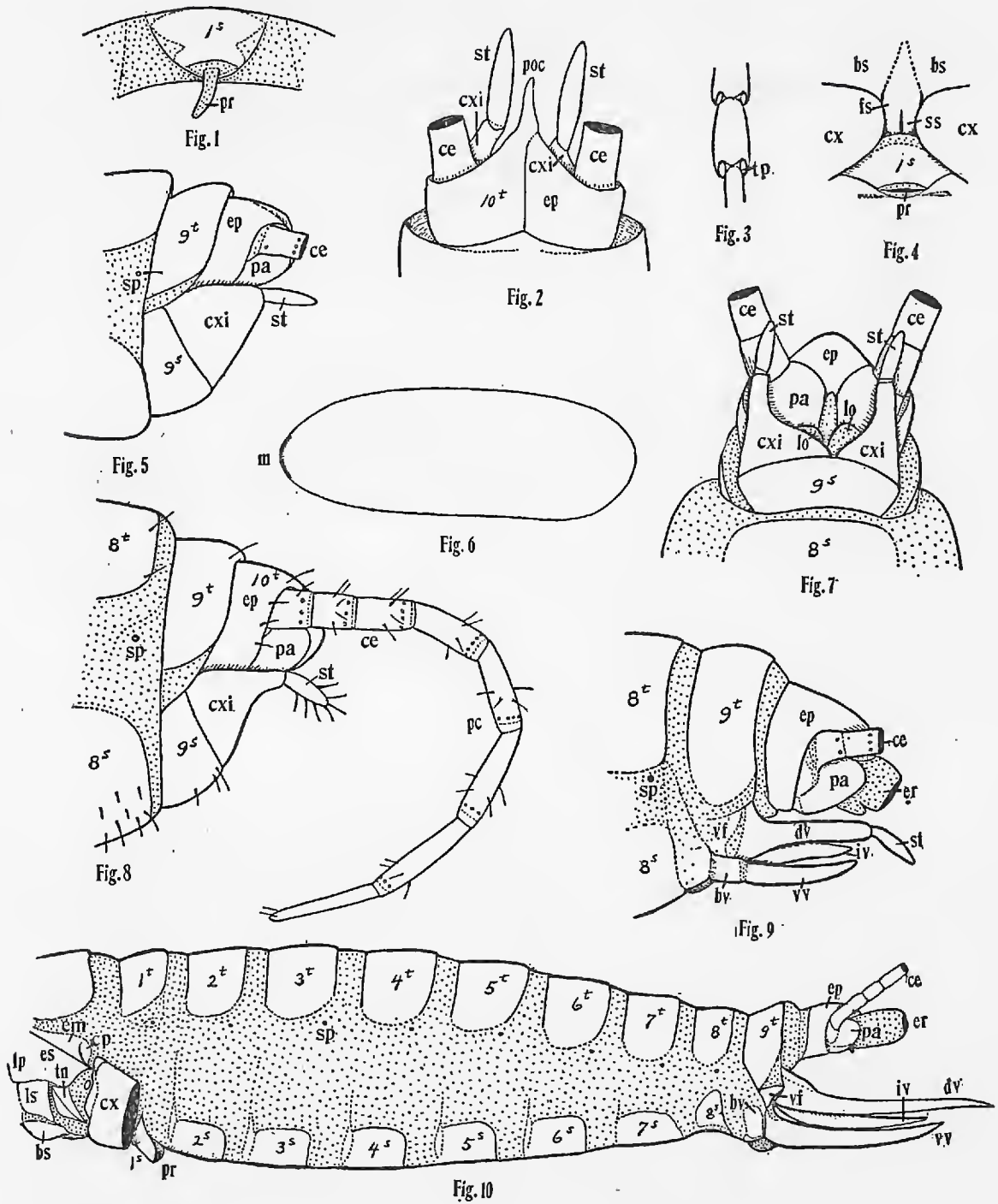
The letter "t" written to the right and above the Arabic numerals indicates the tergite of the segment indicated by the numeral in question, while the letter "s" similarly placed, indicates the corresponding sternite.

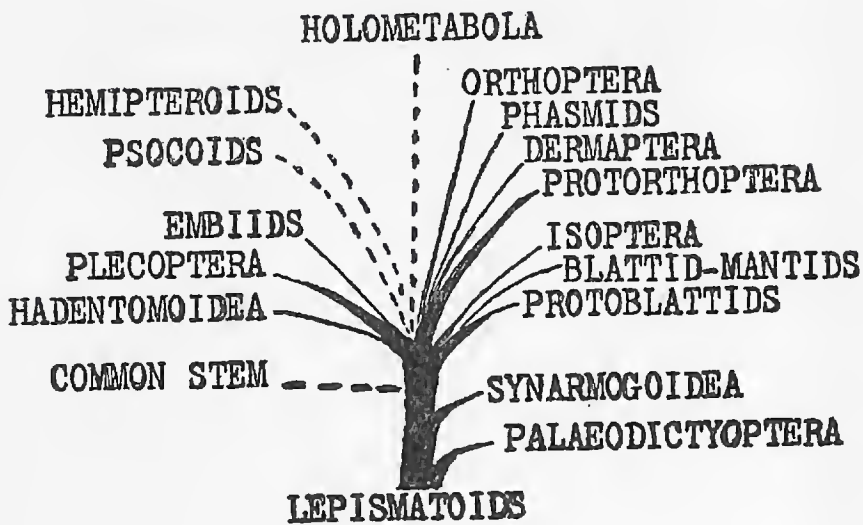
EXPLANATION OF FIGURES

- Fig. 1. Ventral view of first sternite, and its everted repugnatorial structure, of a female nymph of *Grylloblatta barberi*.
- Fig. 2. Dorsal view of the terminal structures of a male of *Galloisiana nipponensis*.
- Fig. 3. Ventral view of a portion of the terminal segments of the tarsus of *Grylloblatta campodeiformis*.
- Fig. 4. Ventral view of posterior region of metasternum and first sternite of an adult female *G. campodeiformis*.
- Fig. 5. Lateral view of terminal structures of an immature male of *G. campodeiformis*.
- Fig. 6. Egg of *G. campodeiformis* viewed from right side with ventral side directed toward top of page.
- Fig. 7. Ventral view of terminal structures of an immature male of *G. barberi*.
- Fig. 8. Lateral view of terminal structure of an immature male of *G. barberi*.

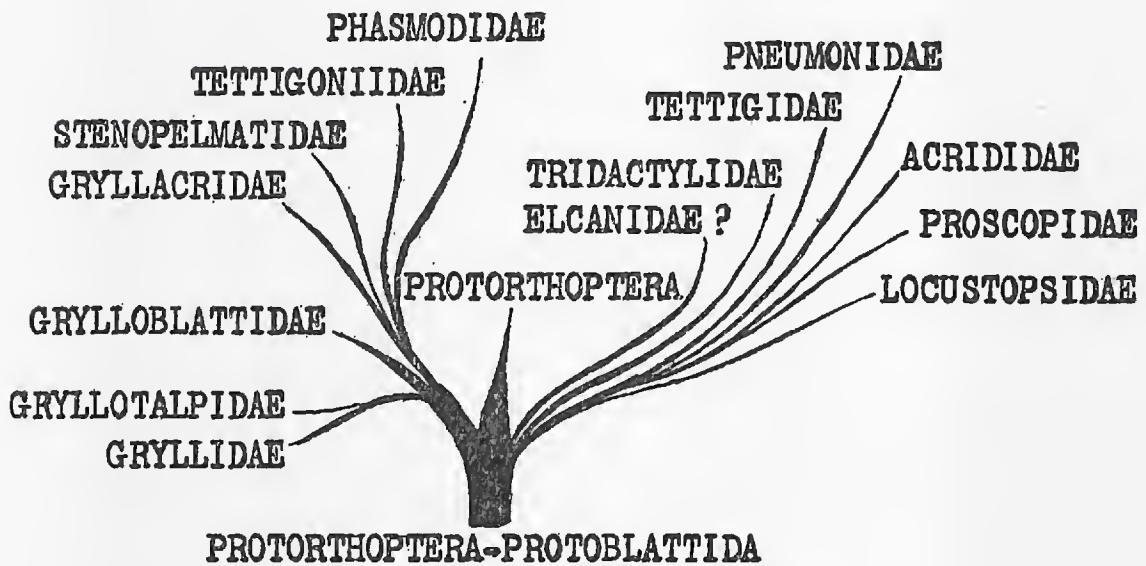
Fig. 9. Lateral view of terminal structures of nymphal female *G. campodeiformis*.

Fig. 10. Lateral view of abdomen of a gravid female of *Grylloblatta campodeiformis*.





Textfigure A



Textfigure B

A CHIRONOMID LEAF-MINER

I have recently reared a Chironomid from serpentine mines in the leaves of semiaquatic species of *Mimulus* and *Veronica*, found at Berkeley, California, and an attempt is now being made to secure the details for a paper illustrating its life history. A careful search through the literature reveals no reference to a leaf-mining habit in the families of the Orthorrhapha. A recent letter to Dr. J. H. Comstock, which he referred to Johannsen, brought the statement that no Chironomid was known to be a leaf-miner although one was known to produce grooves in leaves.—Wyatt W. Jones.